ELECTROPHORETIC STUDY OF CUTTHROAT TROUT POPULATIONS IN UTAH

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ABSTRACT.—Thirty-nine Utah streams were sampled for cutthroat trout. Of these, 31 contain cutthroat or cutthroat/rainbow hybrid populations. By using starch gel electrophoresis, these populations were segregated into three groups. One group consisted predominately of fish from the Sevier River (of the Bonneville Basin) and Colorado drainages. A second was primarily populations from the Bear River Drainage (Bonneville Basin) as well as some scattered populations along the Wasatch Front (Bonneville Basin). The third consisted of Wasatch Front populations and populations that have hybridized with rainbow trout. Since different subspecies of cutthroat trout are native to the Colorado and Bonneville drainages, one would expect the populations from within the Bonneville Basin to be more similar to one another and less similar to the Colorado River populations. That this did not occur raises questions concerning the evolutionary relationships of the subspecies and the populations. It is clear that at least a northern (Bear River) and southern (Sevier River) form of the Bonneville cutthroat exists. The Wasatch Front may represent an intermediate zone where these two forms intergrade.

Salmo clarki, the cutthroat trout, had the most extensive continental distribution of the western North American native trout (Salmonidae, *Salmo*). Behnke (1981) tentatively recognized 15 subspecies of cutthroat trout associated with three major phyletic groups: a coastal cutthroat trout, *S. clarki clarki*, characterized by 68 to 70 chromosomes (Gold et al. 1977); an interior cutthroat trout, *S. c. lewisi*, native to the upper Columbia River, upper Missouri River, and the South Saskatchewan drainages, characterized by 66 chromosomes (Loudenslager and Thorgaard 1979); and a group of subspecies derived from the Yellowstone cutthroat trout, *S. c. bouvieri*, which inhabit the upper Snake River, Yellowstone River, the Great Basin, Colorado River, South Platte River, and Rio Grande drainages. These are characterized by 64 chromosomes (Loudenslager and Thorgaard 1979).

Utah's waters originally supported three cutthroat trout subspecies—the Yellowstone, *S. c. bouvieri*, the Colorado River, *S. c. pleuriticus*, and the Bonneville, *S. c. utah*. The Yellowstone cutthroat is native in the Raft River drainage of northwestern Utah but has now been introduced throughout Utah. The headwaters of the Colorado River Basin (the Green River) downstream to the Dirty Devil River, Utah, on the west and the San Juan drainage of Colorado, New Mexico, and Arizona on the east composed the original range of the Colorado River cutthroat (Fig. 1). This trout has been severely impacted by man and is now considered threatened (Miller 1972). The Bonneville Basin (Fig. 1), situated on the eastern edge of the Great Basin, represents the drainage basin of Pleistocene Lake Bonneville. This basin comprises the original range of the Bonneville cutthroat trout, *S. c. utah*. Until recently the Bonneville cutthroat was thought to be extinct or so hybridized with introduced trout that it was unrecognizable. However, Hickman (1978) located 15 relict populations in Utah, Nevada, and Wyoming, and a sizable sport fishery has now been developed on what may be a native population in Bear Lake at the Utah-Idaho border.

The present distribution of cutthroat trout within the Bonneville Basin is restricted to isolated lakes and tributaries where suitable habitat remained following the desiccation of pluvial Lake Bonneville. Three morphologically and ecologically differentiated groups of populations, associated with the Snake Valley region on the Nevada-Utah border, the Bear River drainage in Wyoming, Idaho, and Utah, and the central Bonneville Basin proper, are currently recognized (Hickman and Duff 1978, Behnke 1981). In addition to the ecological and morphological differentiation of these

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Fig. 1. Major drainage basins in the Utah area. The cross-hatched area represents the Bonneville stage of Lake Bonneville during the Wisconsin glacial period.

population groups, there is evidence of genetic divergence. Klar and Stalnaker (1979) reported a distinctive LDH allele in the Snake Valley population group. Gall and Loudenslager (1981), using 36 protein loci, compared three populations from the Bear River drainage and four populations from the Snake Valley with each other and representative *S. c. bouvieri*, *S. c. pleuriticus*, and *S. c. henshawi*. They reported little genetic differentiation within the Bear River or Snake Valley population groups but substantial differentiation between them. Moreover, the Bear River populations were more similar genetically to *S. c. bouvieri*, and the Snake Valley populations were more similar to *S. c. pleuriticus* than the Bear River and Snake Valley groups were to each other.

In this paper we present results of an electrophoretic analysis of Utah cutthroat trout populations from drainage systems not previously surveyed, using the protein systems that distinguish Snake Valley and Bear River cutthroat trout from each other and rainbow trout, *S. gairdneri* (Gall and Loudenslager 1981). The objectives were to evaluate the genetic relatedness of these populations and identify hybridization between native cutthroat and introduced rainbow trout.

METHODS

Thirty-nine Utah streams located in the Wasatch-Cache, Uinta, Manti-La Sal and Fish Lake National Forests were examined (Fig. 2, Table 1). Both electrofishing and hook and line were used to collect fish. Eight streams lacked cutthroat trout populations. A total of 550 trout from the remaining 31 streams were examined. Fish were frozen in the field on dry ice and returned to Brigham Young University for processing. Following processing, specimens were preserved in formalin and stored in 40% isopropyl alcohol.

Tissue samples were homogenized in 0.25 M sucrose and centrifuged at 30,000 x g for 15 minutes. The resulting supernatant was analyzed with horizontal starch-gel electrophoresis. Four protein systems encoded by six loci were examined: tripeptide aminopeptidase (LGG; EC 3.4.11.4) from muscle tissue, isocitrate dehydrogenase (IDH-3,4; EC 1.1.1.42) from liver tissue, malic enzyme (ME; EC 1.1.1.40) from liver tissue, and sorbitol dehydrogenase (SDH-1,2; EC 1.1.1.14) from liver tissue (Gall and Loudenslager 1981).

Loci are designated using the nomenclature of Allendorf and Utter (1978). An abbreviation that corresponds to the name of a protein designates each locus. Multiple forms of a protein are designated with the least anodally migrating locus as −1, the next −2, and so on. Allelic variants are designated according to the relative mobility of their products, with the most common allele in *S. gairdneri* designated 100.

Allelic frequencies were determined from the protein bands. A matrix of similarities between populations based on Nei's genetic identity index (Nei 1972) was clustered with the NTSYS statistical package. The unweighted pair-group method using arithmetic averages (UPGMA), cluster algorithm was used (Sneath and Sokal 1973).

RESULTS AND DISCUSSION

Polymorphism was found in five of the six loci examined: GCP, IDH-3, ME, and SDH-1,2. Allelic frequencies for these loci are given in Table 2. All of the polymorphisms have been previously described in cutthroat trout (Loudenslager and Gall, 1980; Gall and Loudenslager, 1981).

Evidence of hybridization with hatchery rainbow trout, Salmo gairdneri.— If parental species are monomorphic for different alleles at a locus, or are polymorphic but share no alleles, then that locus can be used to distinguish the parental species and their hybrids (Gall and Loudenslager 1981). Two loci, GCP and ME, examined in the present study can be used to distinguish cutthroat trout, rainbow trout, and their hybrids. The GCP locus had two alleles, GCP (160) and GCP (100). The GCP (160) allele was previously reported to be: monomorphic in *S. c. bouvieri*, *S. c. utah*, and *S. c. pleuriticus* and absent in *S. gairdneri* (Gall and Loudenslager 1981), whereas the GCP (100) allele is the common allele in hatchery *S. gairdneri* (Gall and Loudenslager 1981). Similarly, the ME locus had two alleles, ME (125) and ME (100). ME (125) is monomorphic in *S. c. bouvieri*, *S. c. utah*, and *S. c. pleuriticus* and absent in hatchery *S. gairdneri*, whereas ME (100) is the common

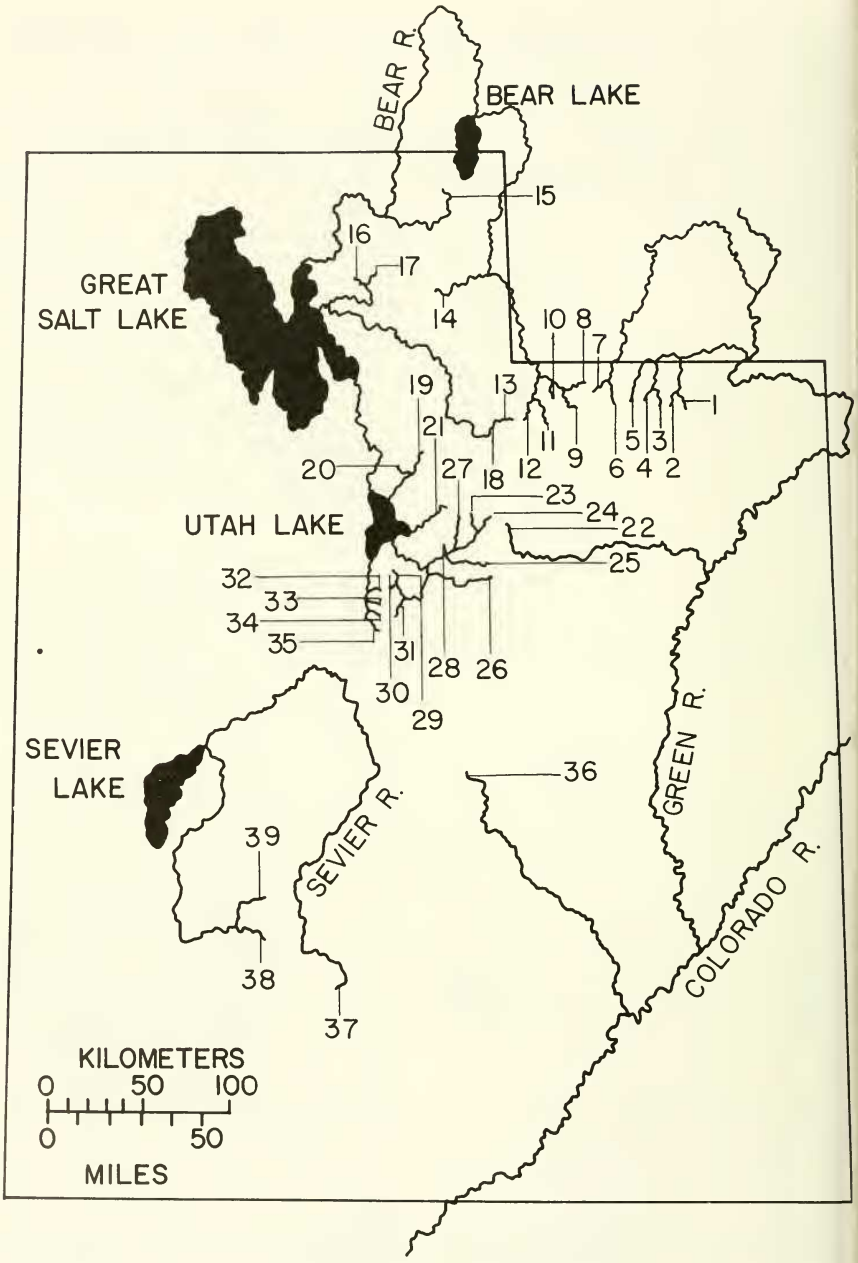

Fig. 2. Location of the 39 streams examined in this study. See Table 1 for the stream name and drainage basin.

TABLE 1. Localities and numbers of trout collected.

Sample number	Sample site	Drainage	Major drainage	Number of specimens
1.	Kabell Creek	Green River	Colorado River	4
2.	Thompson Creek	Green River	Colorado River	16
3.	M. Fk. Beaver Creek	Green River	Colorado River	9
4.	W. Fk. Beaver Creek	Green River	Colorado River	20
5.	Joulious Creek	Green River	Colorado River	17
6.	M. Fk. Blacks Creek	Green River	Colorado River	24
7.	Brush Creek	Green River	Colorado River	22
8.	McKenzie Creek	Bear River	Bonneville Basin	12
9.	Mill Creek	Bear River	Bonneville Basin	22
10.	Carter Creek	Bear River	Bonneville Basin	17
11.	Boundary Creek	Bear River	Bonneville Basin	20
12.	Meadow Creek	Bear River	Bonneville Basin	19
13.	Moffit Creek	Weber River	Bonneville Basin	18
14.	Sugarpine Creek	Bear River	Bonneville Basin	19
15.	Bunchgrass Creek	Logan River	Bonneville Basin	19
16.	Durfee Creek	Ogden River	Bonneville Basin	0
17.	Greetsen Creek	Ogden River	Bonneville Basin	3
18.	Red Pine Creek	Weber River	Bonneville Basin	18
19.	N. Fk. Amer. Fk. River	Utah Lake	Bonneville Basin	5
20.	Silver Creek	Utah Lake	Bonneville Basin	0
21.	L. Fk. Hobble Creek	Utah Lake	Bonneville Basin	21
22.	Strawberry River	Green River	Colorado River	60
23.	Shinglemill Creek	Spanish Fork	Bonneville Basin	16
24.	Chase Creek	Spanish Fork	Bonneville Basin	4
25.	Fifth Water Creek	Spanish Fork	Bonneville Basin	11
26.	Indian Creek	Spanish Fork	Bonneville Basin	0
27.	Wanrhodes Creek	Spanish Fork	Bonneville Basin	11
28.	Little Diamond Creek	Spanish Fork	Bonneville Basin	17
29.	Tie Fork Creek	Spanish Fork	Bonneville Basin	0
30.	Holman Creek	Spanish Fork	Bonneville Basin	27
31.	Nebo Creek	Spanish Fork	Bonneville Basin	23
32.	Mendenhall Creek	Utah Lake	Bonneville Basin	0
33.	North Creek	Utah Lake	Bonneville Basin	0
34.	Bear Canyon Creek	Utah Lake	Bonneville Basin	0
35.	Willow Creek	Utah Lake	Bonneville Basin	0
36.	Muddy Creek	Dirty Devil River	Colorado River	5
37.	Deep Creek	Sevier River	Bonneville Basin	16
38.	Hy Hunt Creek	Sevier River	Bonneville Basin	25
39.	N. Fk. North Creek	Sevier River	Bonneville Basin	30

allele in hatchery *S. gairdneri*. Individuals representative of the parental species will be homozygous for their respective diagnostic alleles, F_1 hybrids will be heterozygous for both loci, and F_2 or backcross individuals will possess a mixture of heterozygous and homozygous diagnostic loci. Evidence for hybridization cannot be based on allele frequencies alone but requires classification of individuals based on a composite biochemical phenotype. This is because composite phenotypes could indicate the presence of both parental species without hybridization.

Of the Utah cutthroat trout populations sampled, seven were found that had an apparent introgression of rainbow trout alleles: Thompson, Mill, Boundary, Bunchgrass, Wanrhodes, Nebo, and Hy-Hunt Creeks. Using the composite enzyme phenotype, no sample included rainbow trout, *Salmo gairdneri*.

Genetic differentiation and relationships among Utah cutthroat trout populations.— An inspection of allelic frequencies (Table 2) indicates that the SDH-1 locus is primarily responsible for differences among Utah cutthroat trout populations (after hybridization with rainbow trout is considered). Cutthroat trout populations in the Colorado River drainage are dichotomous for SDH-1 allele frequencies. Middle Fork Beaver, West Fork Beaver, Joulious, Middle Fork Blacks, and

TABLE 2. Allelic frequencies of 6 loci for 31 trout populations.

Locus		Streams Stream number Kabell 1	Thompson 2	M. Fk. Beaver 3	W. Fk. Beaver 4	Joulious 5	M. Fk. Blacks 6	Brush 7	McKenzie 8
SDH-1	100	——	——	——	——	——	——	——	——
	40	0.63	——	0.05	0.02	0.18	0.12	0.02	1.00
	0	0.37	1.00	0.95	0.98	0.82	0.88	0.98	——
SDH-2	250	——	——	——	——	——	——	——	——
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
IDH-3	170	——	——	——	——	——	——	——	——
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	60	——	——	——	——	——	——	——	——
IDH-4	140	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
LGG	160	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	100	——	——	——	——	——	——	——	——
ME	125	1.00	0.97	1.00	1.00	1.00	1.00	1.00	1.00
	100	——	0.03	——	——	——	——	——	——

Table 2 continued.

Locus		Streams Stream number Mill 9	Carter 10	Boundary 11	Meadow 12	Moffit 13	Sugarpine 14	Bunchgrass 15	Greetsen 17
SDH-1	100	——	——	——	——	——	——	——	——
	40	0.55	1.00	1.00	1.00	0.03	1.00	1.00	0.17
	0	0.45	——	——	——	0.97	——	——	0.83
SDH-2	250	——	——	——	0.13	——	——	——	——
	100	1.00	1.00	1.00	0.87	1.00	1.00	1.00	1.00
IDH-3	170	——	——	0.11	0.03	0.08	——	——	——
	100	1.00	1.00	0.89	0.97	0.92	1.00	0.97	1.00
	60	——	——	——	——	——	——	0.03	——
IDH-4	140	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
LGG	160	0.95	1.00	0.68	1.00	1.00	1.00	1.00	1.00
	100	0.05	——	0.32	——	——	——	——	——
ME	125	1.00	1.00	0.75	1.00	1.00	1.00	0.97	1.00
	100	——	——	0.25	——	——	——	0.03	——

Brush creeks have a high frequency of the SDH-1 (0) allele ($\bar{x} = 0.922$), whereas Kabell Creek, Strawberry River, and Muddy Creek have intermediate frequencies of the SDH-1 (0) allele ($\bar{x} = 0.49$). Gall and Loudenslager (1981) sampled *S. c. pleuriticus* from two locations in Wyoming and found the populations monomorphic for the SDH-1 (0) allele. The intermediate frequency of SDH-1 (40) in Kabell Creek, Strawberry River, and Muddy Creek could be due to natural selection, genetic drift, or hybridization with stocked cutthroat trout. Since Yellowstone cutthroat trout, *S. c. bouvieri*, are monomorphic for SDH-1 (40) (Loudenslager and Gall 1980), hybridization is a probable cause. The Strawberry River is also a major source of cutthroat eggs for stocking operations throughout the

Table 2 continued.

Locus		Streams Stream number Red Pine 18	N. Fk. Am. Fk. 19	L. Fk. Hobble 21	Strawberry 22	Shinglemill 23	Chase 24	Fifth Water 25	Wanrhodes 27
SDH-1	100	—	—	—	—	—	—	—	—
	40	0.25	0.25	1.00	0.50	0.97	1.00	0.50	0.36
	0	0.75	0.75	—	0.50	0.03	—	0.50	0.64
SDH-2	250	—	—	—	—	—	—	—	—
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
IDH-3	170	—	—	—	0.01	—	—	—	—
	100	1.00	1.00	1.00	0.99	1.00	1.00	1.00	0.95
	60	—	—	—	—	—	—	—	0.05
IDH-4	140	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
LGG	160	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.91
	100	—	—	—	—	—	—	—	0.09
ME	125	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.91
	100	—	—	—	—	—	—	—	0.09

Table 2 continued.

Locus		Streams Stream numbers Little Diamond 28	Holman 30	Nebo 31	Muddy 36	Deep 37	Hy Hunt 38	N. Fk. North 39
SDH-1	100	—	—	—	—	—	—	—
	40	0.35	0.85	0.54	0.40	—	0.20	—
	0	0.65	0.15	0.46	0.60	1.00	0.80	1.00
SDH-2	250	—	—	—	—	—	—	—
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00
IDH-3	170	—	—	—	—	—	0.04	—
	100	1.00	1.00	1.00	1.00	1.00	0.96	1.00
	60	—	—	—	—	—	—	—
IDH-4	140	1.00	1.00	1.00	1.00	1.00	1.00	1.00
LGG	160	1.00	1.00	0.87	1.00	1.00	0.80	1.00
	100	—	—	0.13	—	—	0.20	—
ME	125	1.00	1.00	0.91	1.00	1.00	0.86	1.00
	100	—	—	0.09	—	—	0.14	—

state of Utah. The stocking of fish from this population could change allele frequencies in native populations.

Within the Bonneville Basin, cutthroat trout populations were sampled from the Bear River drainage, along the Wasatch Front (Weber and Utah lake drainage), and the Sevier River drainage (Fig. 1). The four Bear River drainage populations not influenced by rainbow trout hybridization were monomorphic for the SDH-1 (40) allele. This supports previous observations that Bear River drainage cutthroat trout were monomorphic for SDH-1 (40) (Gall and Loudenslager 1981). In contrast, both the Deep Creek and North Fork of North Creek populations from the Sevier River drainage were monomorphic for the SDH-1 (0) allele. The SDH-1 allele frequen-

TABLE 3. Genetic identity and distance values for pairwise comparisons of the 31 trout populations sampled. Identity values are above the diagonal, and distance values are below the diagonal.

Stream	No.	1	2	3	4	5	6	7	8	9	10	11	12	13
Kabell	1	—	.931	.942	.936	.964	.954	.936	.977	.998	.977	.942	.973	.936
Thompson	2	.071	—	.999	1.00	.995	.998	1.00	.832	.947	.832	.790	.825	.999
M. Fk. Beaver	3	.060	.001	—	1.00	.997	.999	1.00	.848	.956	.848	.805	.842	.999
W. Fk. Beaver	4	.066	.000	.000	—	.996	.998	1.00	.839	.951	.839	.796	.833	.999
Joulious	5	.037	.006	.003	.004	—	.999	.996	.885	.975	.885	.843	.879	.995
M. Fk. Blacks	6	.047	.003	.001	.002	.001	—	.998	.869	.967	.869	.826	.862	.998
Brush	7	.066	.000	.000	.000	.004	.002	—	.839	.951	.839	.796	.833	.999
McKenzie	8	.023	.184	.164	.175	.122	.141	.175	—	.965	1.00	.972	.997	.840
Mill	9	.002	.054	.045	.050	.025	.034	.050	.035	—	.965	.934	.960	.951
Carter	10	.023	.184	.164	.175	.122	.141	.175	.000	.035	—	.972	.997	.840
Boundary	11	.060	.235	.217	.229	.171	.191	.229	.029	.069	.029	—	.967	.797
Meadow	12	.028	.192	.172	.183	.129	.148	.183	.003	.041	.003	.034	—	.833
Moffit	13	.067	.001	.001	.001	.005	.003	.001	.175	.051	.175	.227	.183	—
Sugarpine	14	.023	.184	.164	.175	.122	.141	.175	.000	.035	.000	.029	.003	.175
Bunchgrass	15	.024	.186	.167	.177	.124	.143	.177	.000	.036	.000	.027	.003	.177
Greetsen	17	.038	.005	.002	.004	.000	.000	.004	.125	.026	.125	.174	.132	.005
Red Pine	18	.026	.011	.007	.009	.001	.003	.009	.101	.017	.101	.148	.108	.010
N. Fk. Am. Fk.	19	.026	.011	.007	.009	.001	.003	.009	.101	.107	.101	.148	.108	.010
L. Fk. Hobble	21	.023	.184	.164	.175	.122	.141	.175	.000	.035	.000	.029	.003	.175
Strawberry	22	.003	.044	.036	.040	.018	.026	.040	.044	.001	.044	.084	.049	.041
Shinglemill	23	.020	.173	.154	.165	.113	.131	.165	.000	.031	.000	.029	.003	.164
Chase	24	.023	.184	.164	.175	.122	.141	.175	.000	.035	.000	.029	.003	.175
Fifth Water	25	.003	.044	.036	.040	.018	.026	.040	.044	.001	.044	.084	.049	.041
Wanrhodes	27	.017	.024	.019	.022	.008	.012	.022	.077	.009	.077	.104	.084	.022
Lt.* Diamond	28	.014	.021	.015	.019	.005	.009	.019	.075	.008	.075	.119	.081	.019
Holman	30	.008	.132	.116	.125	.082	.097	.125	.004	.016	.004	.035	.007	.125
Nebo	31	.006	.055	.047	.052	.028	.036	.052	.040	.002	.040	.058	.047	.053
Muddy	36	.010	.028	.021	.025	.009	.014	.025	.064	.005	.064	.107	.070	.025
Deep	37	.071	.000	.000	.000	.005	.002	.000	.182	.054	.182	.237	.191	.001
Hy Hunt	38	.047	.014	.012	.014	.010	.010	.014	.132	.032	.132	.144	.141	.014
N. Fk. North	39	.071	.000	.000	.000	.005	.002	.000	.182	.054	.182	.237	.191	.001

cies for Wasatch Front populations were highly variable: Moffit Creek had the highest frequency of the SDH-1 (0) allele (0.97), wheras Chase Creek and the Left Fork Hobble Creek were monomorphic for SDH-1 (40). The remaining populations had SDH-1 (0) allele frequencies ranging from 0.03 to 0.83.

A pattern in the SDH-1 allele frequencies is discernible if one includes Loudenslager and Gall's (1980) and Gall and Loudenslager's (1981a, b) findings of populations monomorphic for the SDH-1 (0) allele in four populations native to or derived from the Snake Valley area in western Utah. Populations inhabiting the south and west extremes of the Bonneville Basin are monomorphic for SDH-1 (0), and those in the northeastern region are monomorphic for SDH-1 (40). A zone of intergradation in allele frequency occurs along the Wasatch Front.

Genetic identity and distance were computed (Nei 1972) for all pairwise comparisons of the 31 populations using the six loci surveyed (Table 3). The genetic identity index is an estimate of the proportion of sampled alleles that are identical between paired populations. Genetic distance is an estimate of the net codon differences and a measure of the accumulated allele differences per locus between two populations. Genetic identity in pairwise comparisons of populations ranged from 1.00 in several comparisons to 0.826 between Meadow Creek and North Fork of North Creek. The average genetic identity for pair-wise comparisons of Utah's cutthroat trout was 0.944.

The genetic identity matrix was also used to calculate the mean genetic identity between groups of populations inhabiting different drainage systems (Table 4). In this analysis, populations thought to be hybridized with rainbow trout or Yellowstone cutthroat trout were excluded. Within the Bear River, Colorado River, and Sevier River drainages, genetic identity among localities was high: I = 0.998; 0.998; and 1.00, respectively. In con-

Table 3 continued.

14	15	17	18	19	21	22	23	24	25	27	28	30	31	36	37	38	39
.997	.976	.963	.974	.974	.977	.997	.981	.997	.997	.984	.986	.992	.995	.990	.932	.955	.932
.832	.831	.995	.989	.989	.832	.957	.842	.832	.957	.977	.979	.876	.946	.973	1.00	.986	1.00
.848	.847	.998	.993	.993	.848	.965	.857	.848	.965	.982	.985	.890	.954	.979	1.00	.988	1.00
.839	.838	.996	.991	.991	.839	.961	.848	.839	.961	.979	.982	.882	.949	.976	1.00	.986	1.00
.885	.885	1.00	.999	.999	.885	.982	.893	.885	.982	.992	.995	.922	.973	.992	.995	.990	.995
.869	.867	1.00	.997	.997	.869	.975	.877	.869	.975	.988	.991	.908	.965	.986	.998	.990	.998
.839	.838	.996	.991	.991	.839	.961	.848	.839	.961	.979	.982	.882	.949	.976	1.00	.986	1.00
1.00	1.00	.883	.904	.904	1.00	.957	1.00	1.00	.957	.926	.928	.996	.961	.938	.833	.876	.833
.965	.964	.974	.983	.983	.965	.999	.970	.965	.999	.991	.992	.984	.998	.996	.948	.969	.948
1.00	1.00	.883	.904	.904	1.00	.957	1.00	1.00	.957	.926	.928	.996	.961	.938	.833	.876	.833
.972	.974	.840	.862	.862	.972	.920	.971	.972	.920	.902	.887	.965	.944	.899	.789	.866	.789
.997	.997	.876	.898	.898	.997	.953	.997	.997	.952	.919	.922	.993	.955	.933	.827	.869	.827
.840	.838	.996	.991	.991	.840	.960	.848	.840	.960	.978	.981	.882	.948	.975	.999	.986	.999
—	1.00	.883	.904	.904	1.00	.957	1.00	1.00	.957	.926	.928	.996	.961	.938	.833	.876	.833
.000	—	.881	.902	.902	1.00	.956	1.00	1.00	.956	.926	.926	.996	.960	.937	.831	.876	.831
.125	.127	—	.999	.999	.883	.981	.890	.883	.981	.991	.994	.919	.972	.991	.995	.990	.995
.101	.103	.001	—	1.00	.904	.989	.911	.904	.989	.995	.998	.937	.981	.996	.990	.990	.990
.101	.103	.001	.000	—	.904	.989	.911	.904	.989	.995	.998	.937	.981	.996	.990	.990	.990
.000	.000	.125	.101	.101	—	.957	1.00	1.00	.957	.926	.928	.996	.961	.938	.833	.876	.833
.044	.045	.019	.011	.011	.044	—	.962	.957	1.00	.993	.996	.978	.996	.998	.957	.972	.957
.000	.000	.116	.094	.094	.000	.039	—	1.00	.962	.932	.934	.998	.965	.944	.842	.884	.842
.000	.000	.125	.101	.101	.000	.044	.000	—	.957	.926	.928	.996	.961	.938	.833	.876	.833
.044	.045	.019	.011	.011	.044	.000	.039	.044	—	.993	.996	.978	.996	.998	.957	.972	.957
.077	.077	.009	.005	.005	.077	.007	.071	.077	.007	—	.997	.954	.993	.997	.976	.992	.976
.075	.077	.006	.002	.002	.075	.004	.069	.075	.004	.003	—	.956	.989	1.00	.980	.985	.980
.004	.004	.084	.065	.065	.004	.022	.002	.004	.022	.047	.045	—	.979	.964	.877	.912	.877
.040	.041	.029	.019	.019	.040	.005	.036	.040	.004	.007	.011	.021	—	.992	.946	.976	.946
.064	.065	.009	.004	.004	.064	.002	.058	.064	.002	.003	.000	.036	.008	—	.973	.982	.973
.182	.185	.005	.010	.010	.182	.044	.172	.182	.044	.024	.021	.131	.056	.027	—	.985	1.00
.132	.133	.010	.011	.011	.132	.028	.123	.132	.028	.008	.015	.092	.025	.018	.015	—	.985
.182	.185	.005	.010	.010	.182	.044	.172	.182	.044	.024	.021	.131	.056	.027	.000	.015	—

trast, genetic identity among localities along the Wasatch Front was only 0.928. Pair-wise comparisons of populations from different drainages indicated a high identity between the Sevier River drainage populations and Colorado River populations (I = 0.998). Identity between Bear River drainage populations and either Sevier River drainage samples (I = 0.831) or Colorado River drainage samples (I = 0.855) was much lower. The Wasatch population group had mean identities of 0.940 with the Bear River sites, 0.930 with the Sevier River sites, and 0.941 with the Colorado River sites. These data are similar to those of Loudenslager and Gall (1980b). In addition, they demonstrated a genetic identity of 0.996 between the Bear River Bonneville and Yellowstone cutthroat trout.

The clustering of the genetic identity matrix resulted in three distinct clusters (Fig. 3). Populations in the first cluster were polymorphic for the SDH-1 locus with intermediate frequencies of the (0) and (40) alleles. Included in this cluster were populations hybridized with rainbow and cutthroat populations from the zone of intergradation along the Wasatch Front. The second cluster contained populations from the Colorado River, Sevier River, and Wasatch Front with a high frequency of the SDH-1 (0) allele. The third cluster contained populations from the Bear River drainage and Wasatch Front with a high frequency of the SDH-1 (40) allele.

The similarity between the Colorado and Sevier River Bonneville and between the Bear River Bonneville, and Yellowstone cutthroat strains could be due to common ancestry (closely related) or it could be a result of convergence or drift. However, the dissimilarity between the Bear River and Sevier River forms of the Bonneville cutthroat is definitive. That is, the occurrence of different allelic frequencies must be due to divergent histories of the populations. For example, the headwaters of Meadow Creek (Bear River drainage) and Moffit Creek (Weber River drainage) are less than a kilometer apart, yet the cutthroat populations have SDH-1 (0) frequencies of 0.00 and 0.97, respectively.

Interpretation of the populations along the Wasatch Front is problematic. Urbanization in

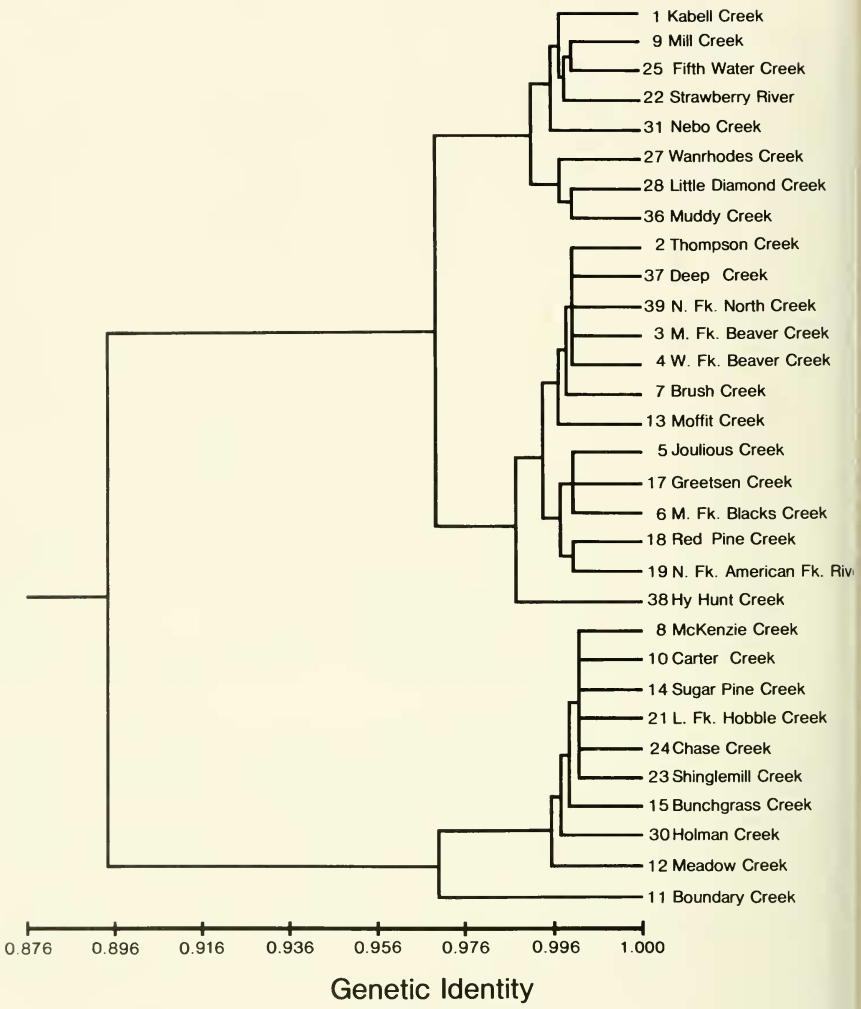

Fig. 3. Cluster dendrogram based on UPGMA clustering of the genetic identity matrix.

TABLE 4. Matrix of genetic identity among cutthroat trout populations from drainages within the Bonneville Basin and Colorado River. The number of sample locations for each drainage is in parenthesis, and within drainage population identity is on the diagonal.

	1	2	3	4
1. Bear R. (4)	.998	.831	.940	.855
2. Sevier R. (2)		1.000	.930	.998
3. Wasatch Front (10)			.928	.941
4. Colorado River (5)				.998

Utah is concentrated along the Wasatch Front. The stocking of nonnative trout has been intense in this area. Although we can reliably identify hybridization with rainbow trout, we are unable to confidently assess hybridization with nonnative cutthroats because of the close genetic relationship between native Bonneville Basin trout and cutthroats from contiguous basins. Whether these popu-

lations were originally polymorphic or monomorphic for SDH-1 is unknown.

Several populations in the Bonneville Basin near Utah Lake had high SDH-1 (40) frequencies. These fish are similar to the Yellowstone cutthroat trout and may have resulted from stocking. The highly polymorphic populations in the area are also likely to have been influenced by the activities of man. For instance, the Diamond Fork drainage (Bonneville basin) receives water diverted from the Strawberry River (Colorado River) drainage. This would allow colonization by Yellowstone-Colorado cutthroat from the Strawberry River into the Diamond Fork drainage and could influence allele frequencies.

Because determining the original geographical variation of the native Utah cutthroat is difficult, all streams that contain cutthroat trout that have not hybridized with rainbow should be given special management consideration. Such streams need not contain monomorphic populations since monomorphism may represent only the extremes of the species variability of the subspecies. Polymorphic populations may still represent the native stocks as long as rainbow hybridization is not evident. This study has advanced our knowledge of the native cutthroat, but much remains to be investigated. One focal area should be the Wasatch Front, where the gradation between the northeastern and southwestern Bonneville forms occurs. Another topic that warrants study is the identification of additional protein systems that separate the Yellowstone from the Bear River Bonneville form and the Snake Valley Bonneville form from the Colorado River cutthroat. These will be instrumental in understanding the taxonomic relationships and variability of the native inland cutthroat trout.

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Literature Cited

ALLENDORF, F. W., AND F. M. UTTER. 1978. Population genetics of fish. Pages 407–454 *in* W. S. Hear and D. J. Randall, eds., Fish physiology. Academic Press, New York. Vol. 8, 786 pp.

BEHNKE, R. J. 1981. Systematic and zoogeographical interpretation of Great Basin trouts. Pages 255–262 *in* R. J. Naiman and D.L. Soltz eds., Biology of fishes of the great American desert. John Wiley Pub., New York. 552 pp.

GALL, G. A. E. AND E. J. LOUDENSLAGER. 1981. Biochemical genetics and systematics of Nevada trout populations. Final Report to Nevada Dept. of Wildlife. 53 pp.

GOLD, J. R., J. C. AVISE, AND G. A. E. GALL. 1977. Chromosome cytology in the cutthroat series *Salmo clarki* (Salmonidae). Cytologia 42:377–382.

HICKMAN, T. J. 1978. Systematic study of the native trout of the Bonneville Basin. Unpublished Masters of Science thesis. Colorado State University, Fort Collins. 122 pp.

HICKMAN, T. J., AND D. A. DUFF. 1978. Current status of cutthroat trout subspecies in the western Bonneville basin. Great Basin Nat. 38: 193–202.

KLAR, G. T., AND C. B. STALNAKER. 1979. Electrophoretic variation in muscle lactate dehydrogenase in Snake Valley cutthroat trout, *Salmo clarki* subsp. Comp. Biochem. Physiol. 64 B: 391–394.

LOUDENSLAGER, E. J., AND G. A. E. GALL. 1980a. Geographic patterns of protein variation and subspeciation in cutthroat trout, *Salmo clarki*. Syst. Zool. 29: 27–42.

———. 1980b. Biochemical systematics of the Bonneville Basin and Colorado River cutthroat. Final Report to the Wyoming Department of Fish and Game. 16 pp.

LOUDENSLAGER, E. J., AND G. H. THORGAARD. 1979. Karyotypic and evolutionary relationships of the Yellowstone (*Salmo clarki bouvieri*) and west-slope (*S. c. lewisi*) cutthroat trout. J. Fish. Res. Board. Canada 36: 630–635.

MILLER, R. R. 1972. Classification of the native trouts of Arizona with the description of a new species, *Salmo apache*. Copeia 1972: 401–422.

NEI, M. 1972. Genetic distance between population. Amer. Natur. 106: 283–292.

SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical Taxonomy. W. H. Freeman Co., San Francisco, California. 573 pp.